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# Cloud shading and fog drip influence the metabolism of a coastal pine ecosystem

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## Abstract

Assessing the ecological importance of clouds has substantial implications for our basic understanding of ecosystems and for predicting how they will respond to a changing climate. This study was conducted in a coastal Bishop pine forest ecosystem that experiences regular cycles of stratus cloud cover and inundation in summer. Our objective was to understand how these clouds impact ecosystem metabolism by contrasting two sites along a gradient of summer stratus cover. The site that was under cloud cover ~15% more of the summer daytime hours had lower air temperatures and evaporation rates, higher soil moisture content, and received more frequent fog drip inputs than the site with less cloud cover. These cloud-driven differences in environmental conditions translated into large differences in plant and microbial activity. Pine trees at the site with greater cloud cover exhibited less water stress in summer, larger basal area growth, and greater rates of sap velocity. The difference in basal area growth between the two sites was largely due to summer growth. Microbial metabolism was highly responsive to fog drip, illustrated by an observed ~3-fold increase in microbial biomass C with increasing summer fog drip. In addition, the site with more cloud cover had greater total soil respiration and a larger fractional contribution from heterotrophic sources. We conclude that clouds are important to the ecological functioning of these coastal forests, providing summer shading and cooling that relieve pine and microbial drought stress as well as regular moisture inputs that elevate plant and microbial metabolism. These findings are important for understanding how these and other seasonally dry coastal ecosystems will respond to predicted changes in stratus cover, rainfall, and temperature.

*Keywords:* $^{13}$C, Bishop pine, cloud shading, decomposition, fog drip, Santa Cruz Island, soil respiration, stratus clouds

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## Introduction

Clouds influence ecological processes by altering fundamental environmental properties such as humidity, temperature, and shortwave irradiance (e.g., Marloth, 1903; Oberlander, 1956; Parsons, 1960). Clouds have been shown to influence the deciduous-conifer transition zones in temperate forests (Richardson *et al*., 2003) as well as the distribution and abundance of frogs and lizards in tropical montane cloud forests (Pounds *et al*., 1999) that are particularly dependent on regular cloud immersion (Still *et al*., 1999). Clouds may be especially important in coastal Mediterranean climate regions such as California, Chile, and South Africa, which experience cool wet winters and hot dry summers, but which typically have a high frequency of stratus cloud cover during summer (Schemenauer & Cereceda, 1991; Dawson, 1998; Weathers, 1999). Stratus clouds are horizontally developed, typically low-altitude clouds, and are the most common cloud type along the California coast in summer, where their bases are typically below 1000 m above sea level. The meteorological definition of low-lying clouds that intersect the ground surface and reduce visibility to below 1000 m is fog (American Meteorological Society, 2000). For our purposes, clouds are considered to be fog whenever they intersect with the land surface, regardless of the impacts on visibility.

Assessing the ecological importance of fog and non-intersecting stratus clouds has large implications for our basic understanding of cloud-dependent ecosystems and how they will respond to a changing climate

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(Still *et al.*, 1999; Scholl *et al.*, 2007; Cereceda *et al.*, 2008). Although predictions about how rainfall will change in California over the next 50 years remain uncertain (Hayhoe *et al.*, 2004), fog and low stratus occurrence might decline as sea-surface temperatures warm (Johnstone & Dawson, 2010). However, trends in coastal stratus behavior may be difficult to predict along California's coast because of the complex way that sea-surface temperature, wind speed, coastal upwelling, and the strength of the overlying atmospheric temperature inversion all interact to influence cloud formation (Williams, 2009; Wang *et al.*, 2010).

To date, most cloud-ecosystem research has focused on the hydrological importance of clouds because they can enhance ecosystem water balance in several ways. First, because fog intersects with land, fog water droplets can accumulate on vegetation and drip to the ground (fog drip), increasing available water particularly in the litter and upper mineral soil layers (Ingraham & Matthews, 1995; Dawson, 1998; Fischer & Still, 2007). Second, fog water and atmospheric water vapor may be directly absorbed by leaves (Rundel, 1982; Boucher *et al.*, 1995; Burgess & Dawson, 2004). Third, stratus reduces irradiance and temperature, thus reducing evaporation from soil and transpiration losses during photosynthesis (Bruijnzeel & Veneklaas, 1998; Burgess & Dawson, 2004; Corbin *et al.*, 2005). Stratus also influences temperature variations at subhourly to annual timescales by shading (shortwave radiation reflection) during the day and insulating (longwave absorption and reradiation) at night (Dai *et al.*, 1999). Overall, compared with clear sky conditions, summer stratus minimizes seasonality and extremes of radiation, temperature, and drought for Mediterranean-type ecosystems (Fischer *et al.*, 2009).

Few studies have directly addressed how clouds influence ecosystem carbon (C) cycling (Bruijnzeel & Veneklaas, 1998; Weathers, 1999). Aboveground, clouds can enhance ecosystem photosynthetic rates by altering the quantity and quality of light within the canopy and in the understory (Gu *et al.*, 1999, 2003; Johnson & Smith, 2006; Brodersen *et al.*, 2008; Still *et al.*, 2009). However, cloud influences on belowground C cycling processes have been almost entirely ignored. Importantly, very small moisture inputs can rapidly stimulate microbial activity in soils of dry ecosystems (Dirks *et al.*, 2010; Carbone *et al.*, 2011). Thus, fog drip, water vapor condensation, and elevated atmospheric humidity associated with increased cloud cover should all enhance ecosystem decomposition rates. Moreover, slight differences in soil water potential can be important to maintaining microbial activity above physical and physiological thresholds within litter and mineral soils (Manzoni *et al.*, 2012), potentially ameliorating microbial drought stress observed in non-cloudy semiarid and arid ecosystems (Schaeffer *et al.*, 2009). Thus, small changes to ecosystem water balance due to the presence or absence of ground-level fog or overlying stratus clouds in coastal ecosystems may substantially alter both plant and microbial metabolism, as well as feedbacks between the two (e.g., Friesen *et al.*, 2011), with potentially large consequences for ecosystem C cycling.

Our objective was to understand how summer fog and low stratus clouds affect ecosystem C cycling on Santa Cruz Island off of southern California, USA. This area gets ~90% of annual rainfall between November and April. In late spring and throughout the summer, however, it is regularly inundated by low stratus clouds, which likely accounts for the occurrence of a relict, drought-sensitive tree species like Bishop pine (*Pinus muricata* D. Don*;* Fischer *et al.*, 2009). Paleodistributions (Pliocene and early Quaternary) of Bishop pines were significantly larger and more widespread when the climate was presumably wetter, cooler, and less seasonal (Chaney & Mason, 1930, 1933; Raven & Axelrod, 1995). Bishop pines on Santa Cruz Island occur near the southernmost range limits of this species, which has only five isolated coastal populations south of Monterey, California (Lanner, 1999; Millar, 1999). For this reason, these Santa Cruz Island populations may be particularly sensitive to small changes in environmental conditions; currently fog drip and cloud shading on Santa Cruz Island mitigate drought stress and soil water deficits that would otherwise increase Bishop pine mortality (Fischer *et al.*, 2009).

We contrasted two sites whose microclimates vary along a gradient of summer stratus cover described in Fischer *et al.* (2009). We observed the response of plant and microbial growth and respiration to fog drip, stratus shading, and overall moisture availability across timescales that ranged from hourly to interannual. Our overarching hypothesis was that stratus clouds and fog immersion relieve moisture stress in the rain-free summer months and reverse typical ecosystem summer dormancy, allowing for enhanced plant and microbial activity and greatly stimulating ecosystem C cycling.

## Materials and methods

### *Site description*

The two research sites on Santa Cruz Island are within Channel Islands National Park, approximately 40 km south of Santa Barbara, California, USA. Located less than 2 km apart, the sites differ in proximity to the ocean and in elevation. The more coastal site was located above Sauces Canyon at lat. 34° 0′ 3.88″N, lon. 119°49′ 4.48″W with an elevation of 296 m. The more inland site was located above Upper Embudo Canyon at lat. 34° 0′ 47.20″N, lon. 119°48′ 11.12″W, at 427 m. The vegetation at both sites is dominated by Bishop pine, with mixed chaparral shrubs, primarily manzanita (*Arctostaphylos insularis)*, and scrub oak (*Quercus pacifica*). The soils are well drained, formed from schist parent material, and classified as loamy-skeletal, mixed, superactive, isomesic Typic Haploxerepts (United States Department of Agriculture, Natural Resources Conservation Service, 2007).

### *Satellite analyses of clouds*

Cloud frequency over each site was calculated with satellite imagery. For this study we did not distinguish cloud altitude, merely the frequency of cloud cover at each site. To understand monthly differences in cloud cover between the sites we used 250 m MODIS imagery collected daily at 10:30 hours PST by the Terra satellite between 2000 and 2006. For each pixel, NASA assigns a quality-control classification indicating clear sky, partial cloud cover, or total cloud cover. We calculated the percent of days per month when the pixels covering our study sites were classified as partially or totally cloudy. To understand diurnal differences in cloud cover between the two sites and summers of our study, we analyzed the 1 km GOES-11 visible band (550–750 nm) imagery collected between 5:00 and 19:00 hours PST (every 30 min) from June to September for both 2008 and 2009. Images were converted from radiance to albedo as described in Bradley *et al.* (2010). We determined a threshold value, 0.2, for which cloud cover occurred at our sites by evaluating the kernel density plots of albedo in conjunction with verification from the Diablo Peak Santa Cruz Island web camera. We then calculated the percent of measurements per 30 min period when the pixels over our study sites were cloud covered.

### *Environmental measurements*

Environmental measurements at each site were logged every 5–15 min. These included air temperature and relative humidity at 1.7 m (HMP45C; Vaisala, Helsinki, Finland), atmospheric pressure (C115; Campbell Scientific, Logan, UT, USA), wind speed and direction (RM Young Wind Monitor), total sun and sky irradiance (LI200; Licor, Lincoln, NE, USA), and photosynthetically active radiation (LI190; Licor). Belowground measurements included litter temperature and relative humidity (HMP44L; Vaisala), and mineral soil temperature (EC95H303W; Thermometrics, Northridge, CA, USA) at 0, 2, 4, 12, and 50 cm depths. Four soil volumetric water content sensors (CS616; Campbell) were located within the top 15 cm of mineral soil at each site. One CS616 was located at 50 cm depth at Upper Embudo, but not at Sauces due to rocky parent material impeding sensor placement. Litter wetness was determined with a leaf wetness sensor placed on the litter surface (C237-L; Campbell). Rainfall and fog drip were measured with tipping bucket rain gauges (TE 525; Texas Electronics, Dallas, TX, USA). Fog drip was measured with a passive harp-style collector connected to a tipping bucket rain gauge, and converted to throughfall depths at both sites, as would be generated from the pine canopy using an empirical site-specific relationship derived in Fischer & Still (2007). Vapor pressure deficit was determined from the difference between actual and saturation vapor pressures, which were calculated by applying dew point and temperature, respectively, to the formulation given in Lowe & Ficke (1974). Potential evapotranspiration was calculated using the Penmann Monteith equation (Snyder & Paw, 2002), which incorporates vapor pressure deficit, wind speed, and net radiation.

### *Pine basal area growth measurements*

Basal area growth at each site was measured with band dendrometers (Series 5; Agricultural Electronics Corp, Tuscon, AZ, USA) installed on 10–15 trees per site (the precise number varied slightly during the measurement period due to equipment failures and new dendrometer installations). Measurements of total change in circumference were recorded on an approximately monthly basis from 2006 through 2009. Change in circumference was converted to change in basal area assuming cylindrical tree trunks. Monthly change in basal area per tree ($cm^2$) was determined for each site by calculating average daily basal area change for all instrumented trees at each site and multiplying daily rate by number of days in the month.

### *Sap velocity measurements*

Sap velocity was measured and logged every 30 min at the base of five pine trees at each site using the heat ratio method (Burgess *et al.*, 2001). Two replicate probesets, each of which measured heat pulse velocity (cm $h^{-1}$) at two radial depths (1.25 and 2.75 cm), were installed on opposite sides of each tree trunk base. Heat pulse velocity was converted to sap velocity (cm $h^{-1}$) following the calculations provided by Burgess *et al.* (2001) and as described in Ambrose *et al.* (2010) after accounting for variations in sapwood properties and correcting for errors associated with probe spacing and wound responses. Sapwood properties, including density, water content, and depth were determined from cores collected near each probeset during wet and dry seasons using a 5 mm diameter increment borer. Sap velocities for each tree were determined as the mean of all four measurement points within each trunk. Sap velocity is reported here as the mean across all trees at each site.

### *$\delta^{13}C$ of root respiration*

Field incubations were used to determine the $\delta^{13}C$ signature of pine root respiration at each site following Carbone *et al.* (2008). Sampling occurred in June, July, and August of 2008, and every one to two months in 2009. Fine roots (<2 mm diameter) were collected from soil blocks (~10 × 10 cm square and 10–15 cm deep) that were excavated from four to five locations at the site. Roots were extracted from the soil, rinsed with water, and placed in two separate airtight 2 L incubation jars. The jars were put in a dark, cool container to maintain temperatures close to *in situ* conditions, and $CO_2$ was allowed to accumulate to at least 2000 ppm (~2 h). The $CO_2$ concentration was measured with an infrared gas analyzer, and air was collected for $\delta^{13}C$ analyses by attaching the jars to evacuated

0.5 L cans. All $CO_2$ samples were extracted from the cans and purified on a vacuum line. The $\delta^{13}C$ of each sample was determined on a Thermo Electron Gas Bench II coupled with a Delta Plus Isotope Ratio Mass Spectrometer at the WM Keck CCAMS facility at UC Irvine. The $\delta^{13}C$ values were corrected for the atmospheric $CO_2$ that was already present in the chamber/jar when sealed using an isotope mixing model.

### *Microbial biomass C, soil C and N*

Litter layer ($n = 4$) and upper 10 cm of mineral soil ($n = 4$) samples were taken at each site three times between June and September during both of 2008 and 2009 with a 5 cm diameter slide hammer corer. Cores were transferred to the laboratory and processed within 48 h. Cores were broken up by hand; rocks, plant material, and fine roots were removed; and soil was passed through a 4 mm sieve. Litter samples were ground to uniform particle size using a coffee grinder. Soil C and N content was measured using an oxidation/reduction element analyzer (Fisons, Inc., Beverly, MA, USA). Microbial biomass C was measured with a chloroform slurry extraction (Fierer & Schimel, 2002) followed by persulfate oxidation and subsequent analysis on a colorimetric autoanalyzer using the $CO_2$ diffusion technique described by Doyle *et al.* (2004) for total organic C. All extractions were performed using 10 g soil (wet weight) and 40 mL extractant in 125 mL glass Erlenmeyer flasks that were acid washed and ashed prior to use. Microbial biomass was calculated as the difference in organic C or N (total N minus inorganic N) between subsamples with and without chloroform added. No correction for chloroform fumigation efficiency was made; therefore the data are presented as the microbial flush of organic C or N. Soil subsamples were measured for soil moisture; gravimetric water content was calculated by oven drying to constant weight at 105 °C.

### *Automated soil respiration measurements*

Soil respiration was measured from June 2008 to October 2009 at each site with automated closed chamber systems described in more detail in Carbone *et al.* (2008). Each system consisted of five dark chambers at each site constructed of white PVC (25 cm inner diameter, 21 cm tall, ~11 L volume). The chambers were located within a 15 m radius from a central controlling box to best capture natural spatial variability within the pine stands. No aboveground portions of living plants were present in the chambers. Individual chambers were continuously measured every 2 h using methods and processing described in Carbone *et al.* (2011). Soil respiration rate is reported here (mg C $m^{-2}$ $h^{-1}$) as the mean of the chambers for each site. Cumulative soil respiration (g C $m^{-2}$) is the aggregated sum of the hourly measurements. Fog drip-stimulated soil respiration was calculated as the C respired above a baseline rate, determined during summer periods without fog drip.

### *Soil respiration $^{14}C$ partitioning*

The fraction of soil respiration derived from live plant roots and their associated microbes (autotrophic) and microbial decomposition of detrital materials (heterotrophic) sources was determined using methods described in Carbone *et al.* (2011). Briefly, a two-end member isotope mixing model (Phillips & Gregg, 2001) was applied to measurements of the $\Delta^{14}C$ of respiration collected from the soil respiration chambers to estimate the fractional contribution (with uncertainty) of each source. For each site, end members were determined with separate field incubations of roots ($n = 10$), and laboratory incubations of soil organic matter cores from each chamber ($n = 5$) as described in Carbone *et al.* (2011). Collections of the $\Delta^{14}C$ in respiration were taken four times over the two summers of 2008 and 2009 from all chambers ($n = 5$) at each site, and $\Delta^{14}C$ measured at the WM Keck CCAMS facility at UC Irvine. The mean partitioning at all time points was multiplied by the cumulative soil respiration from June through September for both years. Error was propagated to include the flux and isotope variability across the chambers, along with partitioning uncertainty.

## Results

### *Cloud cover*

Daily MODIS satellite imagery at 10:30 hours PST demonstrated that from June through September clouds more often covered Sauces than Upper Embudo (Fig. 1a); this difference only occurred consistently in the summer months when low stratus clouds are most common. In winter, from October to March, cloud cover was not consistently different between the sites.

During summer 2008 and 2009, half-hourly GOES satellite imagery between 05:00 and 19:00 hours PST captured the temporal patterns in the daytime cloud cover frequency (though with coarser spatial resolution than the MODIS images). It was most frequently cloudy in the early morning at both Sauces and Upper Embudo (05:00–07:00 hours; Fig. 1b and c). As with the MODIS analyses, the cloud frequency at Sauces was consistently higher than at Upper Embudo in both 2008 (Fig. 1d) and 2009 (Fig. 1e). The difference between the two sites was greater in 2008. In 2009, the primary difference between the sites was in early morning and late afternoon hours. Overall, Sauces and Upper Embudo had clouds overhead during 32% and 25% of daytime hours in 2008, and 28% and 26% of daytime hours in 2009, respectively (Table 1). These satellite observations are in agreement with site-based estimates of cloud shading from measurements of insolation shown below.

Differences in summer cloud cover were associated with measureable differences in environmental factors at the sites. Daily mean air temperature, vapor pressure deficit, insolation, and potential evapotranspiration were all consistently and significantly ($P < 0.05$) lower at Sauces than Upper Embudo during summers 2008 and 2009 (Fig. 2). In addition, Sauces experienced much

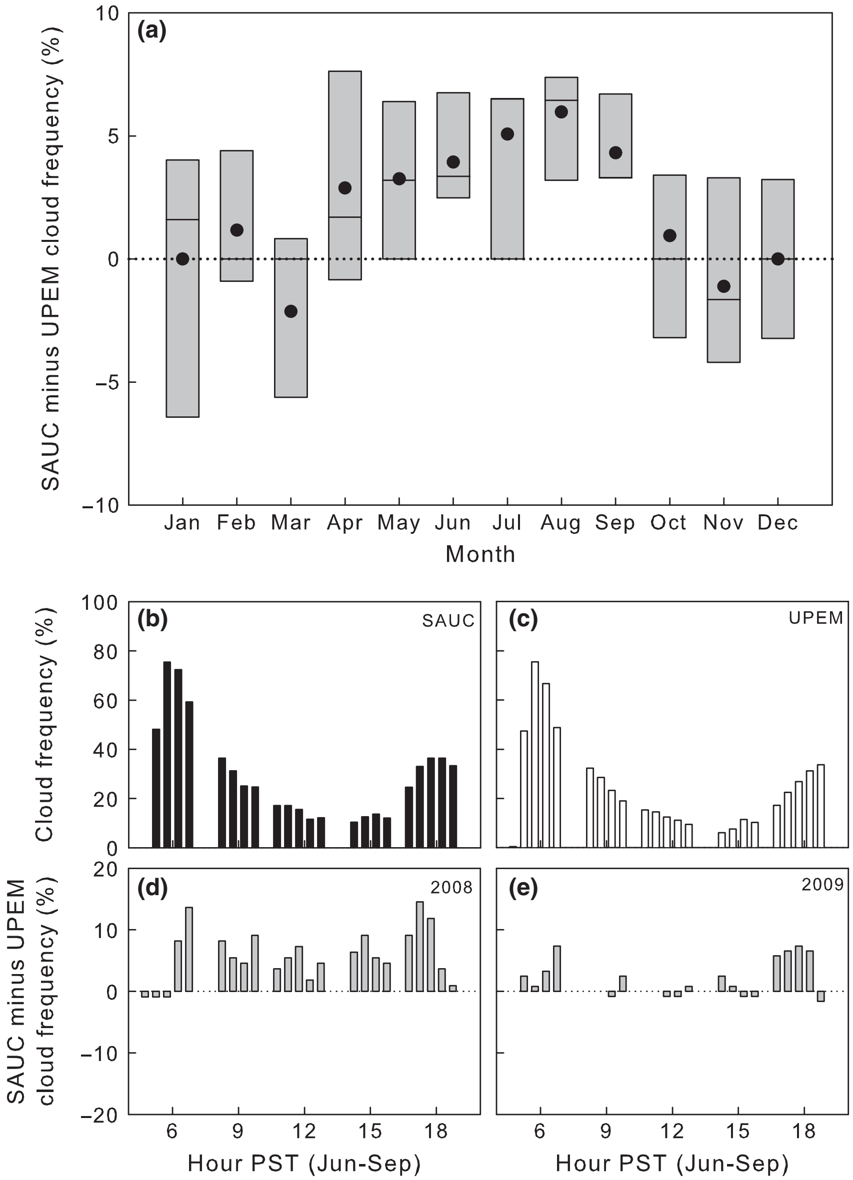

**Fig. 1** (a) Monthly difference in cloud frequency (%) between Sauces (SAUC) and Upper Embudo (UPEM) from 2000 to 2006 derived from daily 10:30 hours PST MODIS Terra satellite imagery. For each box plot, the horizontal line is the median, the edges of the box are the 25th and 75th percentiles, and the filled circle is the mean. Mean cloud frequency in 2008 and 2009 (from 05:00 to 19:00 hours PST) at SAUC (b) and UPEM (c) from June to September derived from half-hourly GOES satellite imagery. Mean difference in cloud frequency between SAUC and UPEM in 2008 (d) and 2009 (e).

smaller variation in summer temperature and vapor pressure deficit than did Upper Embudo; however, the sites had very similar environmental conditions during winter and spring months.

### *Moisture inputs*

Overall, Upper Embudo received greater total precipitation (rainfall plus fog drip) inputs in both years. In 2008, rainfall was slightly below the historic average for the Central Valley of Santa Cruz Island (509 mm) at both sites, and well below average in 2009 (Table 1). Sauces received approximately 75% of the rainfall that Upper Embudo did, likely due to orographic effects on precipitation (Upper Embudo is ~130 m higher than Sauces). Fog drip throughfall, as estimated from fog collectors, was comparable at both sites and was greater in 2009 than 2008.

The frequency of water inputs at both sites was high. Summer fog drip was more frequent at Sauces than

**Table 1** Moisture at Sauces (SAUC) and Upper Embudo (UPEM) in 2008 and 2009 water years (Oct–Sep). Precipitation inputs: rainfall, fog drip throughfall, and total precipitation (mm; water depth). Soil moisture: winter 15 cm mineral soil, summer 15 cm mineral soil, summer 50 cm mineral soil (%). Summer daytime cloud frequency (%; percent of GOES measurements with clouds). Summer fog drip frequency (%; percent of days with fog drip). Litter moisture: summer daytime, summer nighttime (%; percent of continuous 5 min measurements with liquid water on litter surface)

| | 2008 | | 2009 | |
|---|---|---|---|---|
| | SAUC | UPEM | SAUC | UPEM |
| Rainfall (mm) | 391 | 467 | 188 | 276 |
| Fog drip (mm) | 236 | 224 | 326 | 361 |
| Total precipitation (mm) | 627 | 691 | 514 | 637 |
| Winter 15 cm soil moisture (%) | 28.4 | 23.3 | 25.4 | 18.7 |
| Summer 15 cm soil moisture (%) | 18.9 | 14.5 | 23.1 | 15.5 |
| Summer 50 cm soil moisture (%) | – | 47.3 | – | 36.7 |
| Summer daytime cloud cover (%) | 32 | 25 | 28 | 26 |
| Summer fog drip frequency (%) | 52 | 48 | 46 | 42 |
| Summer wet litter daytime (%) | 48 | 32 | 54 | 22 |
| Summer wet litter nighttime (%) | 79 | 63 | 87 | 58 |

Upper Embudo, occurring at Sauces 52% and 46% of days in 2008 and 2009, respectively, and at Upper Embudo, 48% and 42% of days in 2008 and 2009, respectively. Over the course of the year, there was frequent precipitation in these ecosystems (either fog drip or rain), with approximately 75% of these events from fog drip. Fog drip primarily enhanced litter layer moisture; only the larger drip events were detectable in the surface mineral soil moisture sensors.

The surface of the litter layer was wet most of the summer nighttime hours, 79–87% at Sauces and 58–63% at Upper Embudo, consistent with periods when fog drip normally occurs, although this could also result from direct condensation of dew without the presence of fog drip. The litter layer was more often wet at Sauces than at Upper Embudo during both day and night (Table 1). Notably, even though fog drip inputs were greater in 2009 than 2008, Upper Embudo litter was generally drier in 2009, perhaps due to more rapid evaporation due to higher temperatures and vapor pressure deficit in 2009. Surface mineral soil moisture was consistently higher at Sauces than at Upper Embudo, likely due to the greater fog drip inputs and reduced evaporative demand at Sauces. Surface mineral soil moisture was also greater in summer 2009 at both sites, corresponding to enhanced fog drip inputs. In contrast, deeper mineral soil moisture (50 cm) was greater in summer 2008 at Upper Embudo (no 50 cm sensor at Sauces), reflecting more rainfall during the preceding winter.

### *Pine basal area growth*

Annual pine basal area growth rate at Sauces was 16% larger than at Upper Embudo from 2006 to 2009. During this time period, the average monthly change in pine basal area at both Sauces and Upper Embudo was lowest in October (~1 cm$^2$) and highest (4–5 cm$^2$) in March and April (Fig. 3). While basal growth occurred year round at both sites, during summer specifically, basal growth was 55% larger ($P < 0.01$) at Sauces than at Upper Embudo. During November–February, basal growth was 13% larger (not significant) at Upper Embudo, where more rain falls during these months.

### *Sap velocity*

Consistent with the tree growth site differences, sap velocities in the pine trees at Sauces were nearly twice those of Upper Embudo over the entire study period. At both sites, sap velocities declined throughout the summer, and were higher but more variable during the winter and spring seasons in response to periodic rain water inputs. Mean summer sap velocities were 3.1 ± 1.6 and 1.1 ± 0.6 cm h$^{-1}$ in 2008 and 1.0 ± 0.5 and 0.5 ± 0.3 cm h$^{-1}$ (±1 SD across trees) in 2009 for Sauces and Upper Embudo, respectively. Summer sap velocities were significantly higher in 2008 at both sites ($P < 0.01$), and gradually decreased over the summer months with declining mineral soil moisture (Fig. 4a). Daytime fog events resulted in a reduction in pine-sap velocities due to reduced irradiance (Fig. 4b and c), and such events were followed by only small and temporary increases once clear skies returned. In contrast, nighttime fog events generally resulted in no sap velocity response during the following day (Fig. 4b–d; shown for Sauces only). Reverse sap velocity, which would indicate significant foliar uptake of fog water, was not observed at either site.

### *$\delta^{13}CO_2$ of root respiration*

The $\delta^{13}$C of pine root respiration varied strongly across seasons, where mean values were more negative (−26.5%) in the wet winter and less negative (−23.5%) in the dry summer ($P < 0.01$). Differences between the two sites and two summers were also observed in the $\delta^{13}CO_2$ of pine root respiration. In winter, the $\delta^{13}CO_2$

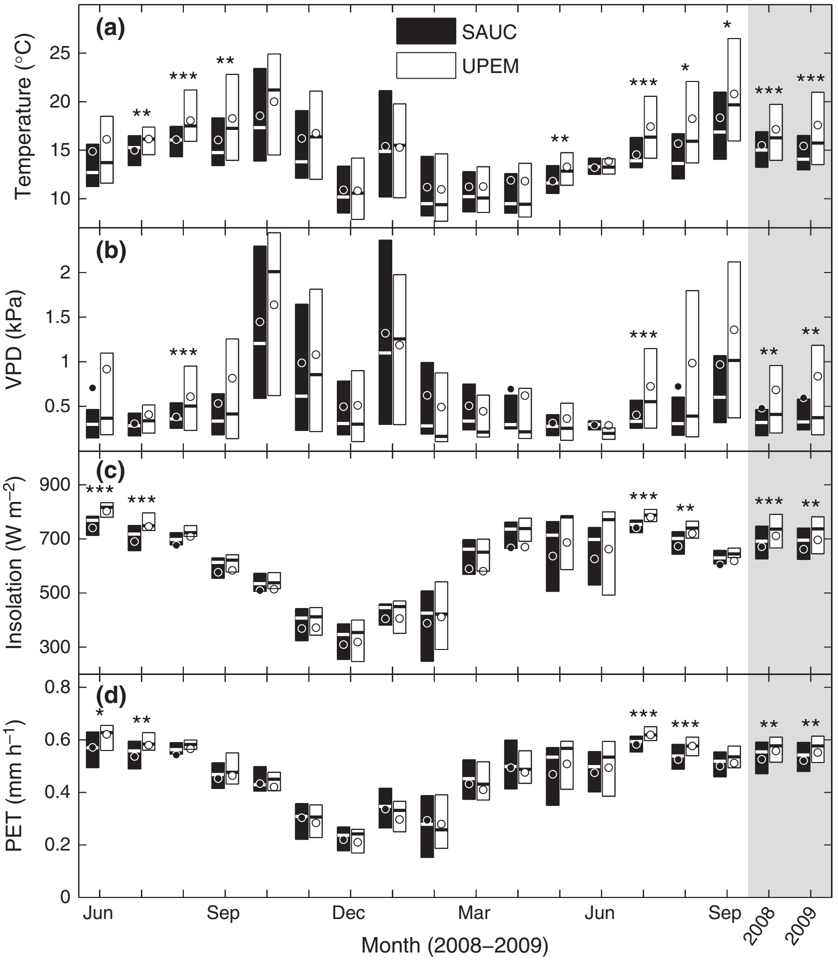

**Fig. 2** Monthly 24 h air temperature (a), 24 h vapor pressure deficit (b), 09:00–17:00 hours insolation (c), and 09:00–17:00 hours potential evapotranspiration (d) at Sauces (SAUC; black) and Upper Embudo (UPEM; white) from June 2008 through September 2009. Box plots in the gray section on the right represent the June–September summer seasons of 2008 and 2009. For box plots, the horizontal line is the median, the edges of the box are the 25th and 75th percentiles, and the circle is the mean. Asterisks indicate significant differences between SAUC and UPEM at the 0.01 (***), 0.05 (**), and 0.1 (*) levels.

values were slightly more negative at Upper Embudo, a difference that was not statistically significant but is consistent with the higher winter rainfall at this site (Table 1). In summer, $\delta^{13}CO_2$ values were significantly ($P < 0.01$) more negative at Sauces (Fig. 5a), with the crossover between the two sites occurring between March and April 2009, and the difference increasing throughout the summer. The largest difference between the two sites was in late summer, where Sauces $\delta^{13}CO_2$ values of root respiration were 1.7% and 1.4% more negative than at Upper Embudo in 2008 and 2009, respectively. Notably, the $\delta^{13}CO_2$ of root respiration was more than 1.5% more negative in the summer of 2008 than 2009 for both sites, consistent with the greater previous winter's rainfall and reduction in plant water stress.

The $\delta^{13}CO_2$ of pine root respiration was negatively correlated with soil moisture at 50 cm depth ($r^2 = 0.85$, $P < 0.01$; Fig. 5b, shown for Upper Embudo only). The $\delta^{13}CO_2$ of pine root respiration also correlated negatively with sap velocity at both sites (in both summer and winter), with the strongest relationship observed between the 5-day mean of sap velocity prior to the root $\delta^{13}C$ measurement (Fig. 5c; $r^2 = 0.90$ and 0.83, $P < 0.01$, for Sauces and Upper Embudo, respectively). The slopes of these regression lines were significantly different from each other ($P < 0.01$); they were steeper at Upper Embudo, consistent with a greater sensitivity of water-use efficiency at sites where water is more limiting (Bowling *et al.*, 2008; Seibt *et al.*, 2008).

### *Microbial biomass and soil properties*

The litter layer and mineral soil at Sauces had lower C and N content in the upper layers (21 ± 2 and 2 ± 0.1%

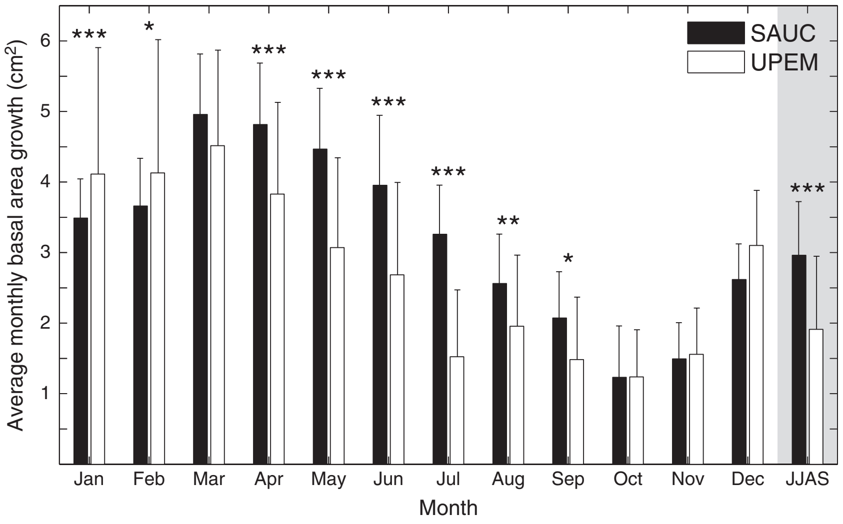

**Fig. 3** Mean monthly change in pine basal area for Sauces (SAUC; black) and Upper Embudo (UPEM; white) for 2006–2009. Error bars indicate 1 SE. Box plot in the gray section represents the average June–September (JJAS) season during 2006–2009. Asterisk symbols represent significant site differences at the 0.01 (***), 0.05 (**), and 0.1 (*) levels.

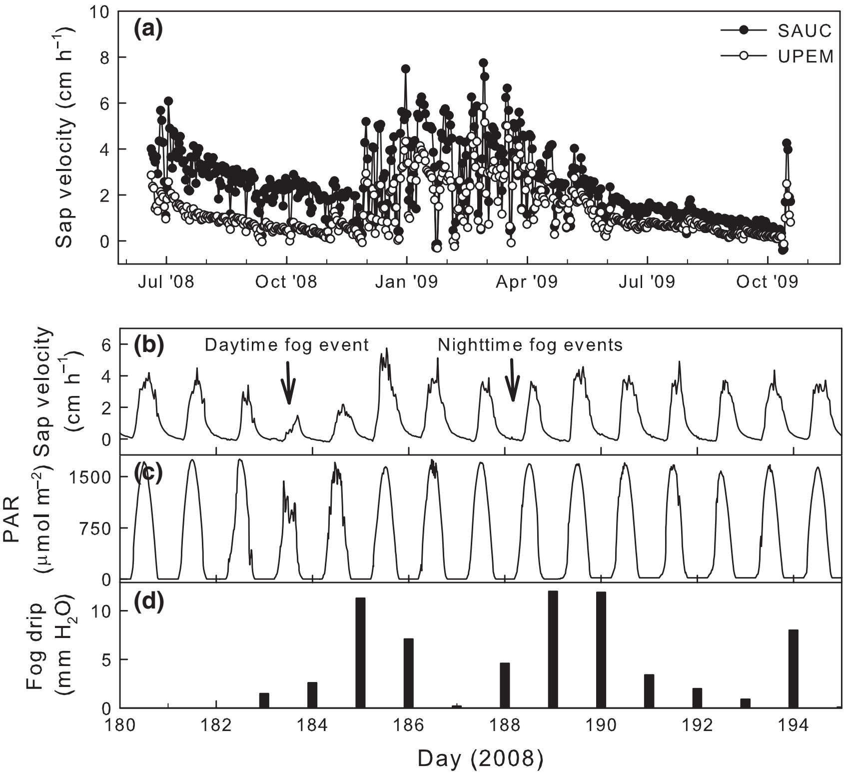

**Fig. 4** (a) Mean pine-sap velocity (cm h$^{-1}$) per day at Sauces (SAUC; black) and Upper Embudo (UPEM; white) from June 2008 to October 2009. (b) Response of SAUC sap velocity to a daytime fog event and nighttime fog events, (c) PAR (μmol m$^{-2}$), and (d) fog drip throughfall (mm $H_2O$) from DOY 180–195 in 2008.

C, and 0.7 ± 0.06 and 0.1 ± 0.005% N, respectively) than Upper Embudo (31 ± 2 and 7 ± 1% C, and 0.9 ± 0.06 and 0.2 ± 0.03% N, respectively; ±1 SE). During the summer, microbial biomass C was similar at Sauces and Upper Embudo (Fig. 6). Microbial biomass C in the litter layer ranged from two to eight times larger than in the mineral soil at both sites. Litter microbial biomass C in summer 2009 was more than three times that of

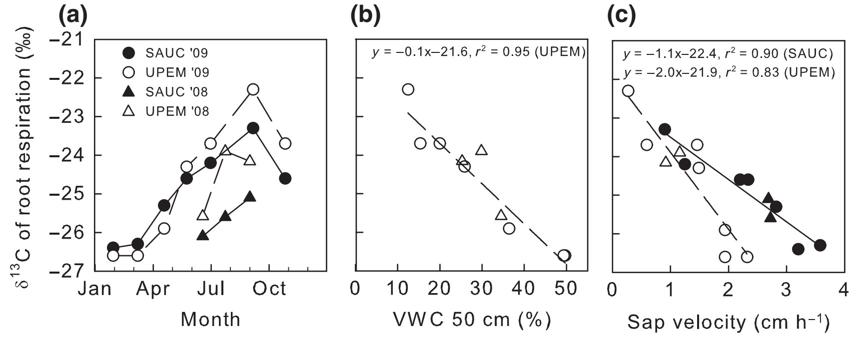

**Fig. 5** (a) The $\delta^{13}$C of pine root respiration in Sauces (SAUC; black) and Upper Embudo (UPEM; white) for 2008 (triangles) and 2009 (circles). (b) Regression between deep (50 cm) volumetric water content (VWC) and the $\delta^{13}$C of pine root respiration at UPEM (dashed line). (c) Regression between pine-sap velocity (cm h$^{-1}$) and the $\delta^{13}$C of pine root respiration at SAUC (solid line) and UPEM (dashed line). Error, smaller than symbols, represents ±1 SD instrument error.

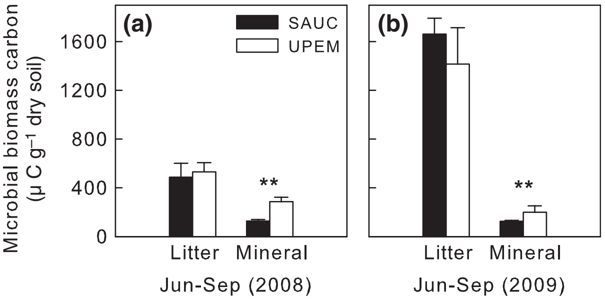

**Fig. 6** Microbial biomass carbon (μ C g$^{-1}$ dry soil) at Sauces (SAUC; black) and Upper Embudo (UPEM; white) for litter and surface mineral horizons in the summer 2008 (a) and summer 2009 (b). Error bars represent 1 SE across ($n$ = 4) replicate cores and ($n$ = 3–4) sampling time points. Asterisks represent significant site differences at the 0.05 (**) level.

summer 2008 at both Sauces and Upper Embudo, consistent with higher summer water inputs from fog drip and warmer temperatures in 2009. Microbial biomass C in the mineral soil did not differ between summers at either site, but it did differ between sites in both summers. Although small relative to the litter, microbial biomass C in the mineral soil at Upper Embudo was significantly larger ($P < 0.05$), and nearly double that of Sauces in both years, and thus made up a greater proportion of the total. The fraction of microbial biomass C in the litter vs. the mineral horizon increased between summer 2008 and 2009, from 77% to 93% at Sauces, and 65 to 85% at Upper Embudo, respectively. This vertical shift in microbial biomass was consistent with greater summer fog drip in 2009, providing greater water inputs to the litter layer.

### *Summer soil respiration*

Summer soil respiration patterns were defined by rapid responses to frequent small water pulses from fog drip (Fig. 7). Mean rates and cumulative soil respiration totals (Fig. 8a and c) were higher at Sauces than at Upper Embudo in both years, with the difference between the two sites increasing throughout the summer, a pattern that parallels the site-level differences in pine basal area growth increments. In 2008, the absence of fog drip in the late summer (September) at Upper Embudo (Fig. 7c) resulted in large differences in soil respiration rates between sites, and cumulative soil respiration was significantly ($P < 0.05$) greater at Sauces than Upper Embudo in September of both years (Fig. 8a and c). Higher mean rates, and greater cumulative soil respiration, were maintained in 2009 than in 2008 at both sites. In 2008, 240 ± 11 and 210 ± 9 g C m$^{-2}$ were respired from Sauces and Upper Embudo, respectively, compared to 341 ± 16 and 232 ± 10 g C m$^{-2}$ (±1 SE across chambers) in 2009. Thus, cumulative soil respiration was approximately 40% greater in 2009 than 2008 at Sauces, but only 10% greater at Upper Embudo. Over both summers, the proportion of dry season respiration that was driven by fog drip was ~45% at Sauces and ~33% at Upper Embudo (Fig. 8a and c), determined by the elevation in soil respiration above a dry baseline rate.

At both sites, most summer soil respiration was from autotrophic sources, but at Sauces, that proportion was less than at Upper Embudo; 58 ± 8% compared to 67 ± 14% (±1 SE). This difference in source partitioning translated into large differences in total C respired at each site from the two sources. In 2008, the sites differed only in heterotrophic respiration, with Sauces respiring ~45% more heterotrophic C than Upper Embudo (Fig. 8b). In 2009, Sauces respired ~30% more autotrophic C and ~90% more heterotrophic C than Upper Embudo, with much of the difference occurring in September (Fig. 8c and d).

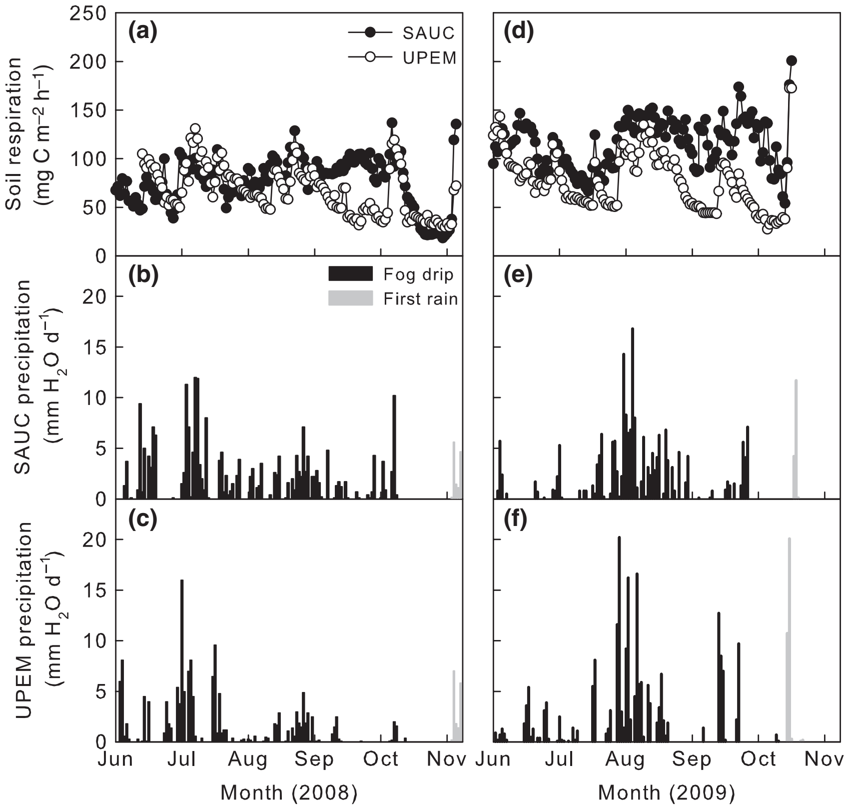

**Fig. 7** Mean soil respiration rates (mg C $m^{-2}$ $h^{-1}$) across ($n$ = 5) chambers at Sauces (SAUC; black circles) and Upper Embudo (UPEM; white circles) from June 1 to the date of first rain for 2008 (a) and 2009 (d). Summer precipitation (mm $H_2O$ $d^{-1}$) for 2008 (b, c) and 2009 (e, f) for SAUC and UPEM, respectively. Fog drip (black bars) and first rains (gray bars).

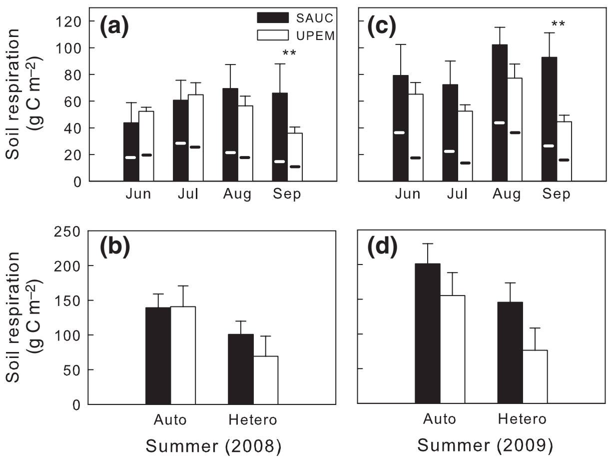

**Fig. 8** Top panels: monthly soil respiration (g C $m^{-2}$) at Sauces (SAUC; black) and Upper Embudo (UPEM; white) in June–September for 2008 (a) and 2009 (c). Fog drip-stimulated soil respiration shown with lines within each bar. Error bars represent 1 SD across ($n$ = 5) chambers. Asterisks represent significant site differences at the 0.05 (**) level. Bottom panels: cumulative summer soil respiration derived from autotrophic and heterotrophic sources at SAUC (black) and UPEM (white) for 2008 (b) and 2009 (d). Error bars represent 1 SE.

## Discussion

### *Environmental conditions*

The difference in summer stratus frequency between Sauces and Upper Embudo results from two key differences in site geography. First, Sauces is located closer to the coast than Upper Embudo. As summer stratus clouds encroach inland in the afternoon as the island cools, and then recede to the ocean as the island warms in the morning, sites nearer to the coast spend more time beneath or within the stratus layer. Second, Sauces is lower in elevation than Upper Embudo, and thus is more often beneath a persistent summer atmospheric temperature inversion (~400–500m; Leipper, 1994; Williams, 2009) that traps coastal stratus clouds.

Differences in summer cloud cover between Sauces and Upper Embudo caused large differences in environmental surface conditions. Greater summer frequency of both overhead and ground-level stratus occurrence at Sauces led to reduced air temperature, vapor pressure deficit, and insolation, and thus evaporative demand. More frequent fog drip and reduced evaporative demand also maintained higher summer litter and soil moisture at Sauces. In contrast, Upper Embudo experienced warmer and more variable summer temperatures, higher potential evapotranspiration rates, and less-frequent fog drip events; it thus had lower summer litter and soil moisture. At both sites, the high frequency of some form of precipitation (fog drip or rainfall) was remarkable for California's dry climate, where a 6-month rainless dry season is common.

Litter and soil moisture at Sauces was higher year round, even though it received less total precipitation (fog drip plus rainfall), compared with Upper Embudo. Thus, the greater water deficit during the summer at Upper Embudo was not fully replenished by prior winter rains and was likely intensified by greater drought. These dry conditions at Upper Embudo may have been exacerbated by increased hydrophobicity and/or soil cracking and preferential flow paths, both of which can decrease soil water retention in the upper soil layers (Sowerby *et al.*, 2008).

### *Pine activity*

Shading from low stratus clouds and regular small water supplements from fog drip help alleviate drought stress and allow for greater summer pine activity at Sauces in comparison to Upper Embudo. Pine trees at Sauces had lower summer water stress (more negative $\delta^{13}$C of root respiration), higher transpiration rates (sap velocities), and greater basal area growth. Differences in pine growth between Sauces and Upper Embudo largely occurred in summer, which we attribute to greater availability of soil moisture left over from subsequent winter rainfall. Low stratus clouds during summer likely preserve rain-derived soil moisture later into the growing season by reducing atmospheric evaporative demand; this occurs through reduced insolation and surface temperatures from both cloud shading and surface evaporative cooling following fog drip events. It is possible that increased cloud cover resulted in greater diffuse light enhancement of photosynthesis at Sauces compared with Upper Embudo. However, given the relatively open nature and low leaf area of the pine stands, we believe this effect was minimal.

Our results indicate that foliar uptake of water from fog deposition, if it does occur, was not substantial enough to induce detectable reverse flow rates at the base of the trees where sap velocity was measured. Reverse flow is a phenomenon that has been documented during the summer fog season in another coastal tree species, the Coast Redwood (Burgess & Dawson, 2004). However, additional measurements at the leaf level are necessary to document the occurrence, potential magnitude, and physiological consequences of foliar water uptake in these trees. Bishop pine is known to have cuticular waxes lining the stomatal pits (Lanner, 1999), and the amount and composition of cuticular wax is known to play an important role in water fluxes across the epidermis by determining foliar hydrophobicity in pines (Leyton & Armitage, 1968; Kerstiens, 1996).

In addition, pines did not appear to rely heavily on fog drip in summer, as most fog drip events did not substantially increase sap velocities nor prevent a gradual decline in sap velocities throughout summer at both sites. However, there was evidence of small, temporary sap velocity responses to larger fog events. Active pine roots deeper in the mineral soil profile probably cannot access fog drip unless the drip event is large enough to cause infiltration below the litter layer and upper mineral soil. This result is in agreement with the study of Carbone *et al.* (2011), which demonstrated no pine-sap velocity response to experimental summer water additions. Prior winter rainfall and deep soil moisture appeared to be more important to summer pine activity as demonstrated by decreased sap velocity in summer 2009 compared with 2008, and lower summer sap velocity at Upper Embudo relative to Sauces. Thus, the largest impact of summer stratus clouds on plant metabolism therefore appears to be reduced summer evaporative demand, which helps preserve soil moisture deposited by cold-season precipitation. This corroborates previous results showing that prior winter rainfall explains the majority of growth variability in nearby Torrey pine forests (Biondi *et al.*, 1997; Williams *et al.*, 2008) as well as new research implicating warm-season atmospheric evaporative demand as a primary driver of forest drought stress throughout the southwestern United States (Williams *et al.*, 2012).

The strong deeper soil moisture control on pine activity was also revealed in the seasonality of the $\delta^{13}$C of root respiration. These isotopic patterns may be explained by the decline in deep soil moisture and resulting lower sap velocities from winter to summer, in which the $\delta^{13}$C of new assimilates increases due to greater stomatal closure from water stress (Farquhar *et al.*, 1982). The seasonal changes in the $\delta^{13}$C of new assimilates are thus reflected in the substrate used for pine root respiration, exhibiting lower water stress in pines at Sauces in the summer. Similar seasonal patterns in the $\delta^{13}$C of respiration have been observed in other water-limited ecosystems (Schaeffer *et al.*, 2008; Wingate *et al.*, 2010; Riveros-Iregui *et al.*, 2011). However, the mean age of C respired by roots in this ecosystem was ~2.5 years (determined by $\Delta^{14}$C on the same samples – Carbone *et al.*, 2011). These two coinciding results are not contradictory, and support previous research that a combination of C pools (recent photosynthetic products and storage C) fuel root respiration (Carbone & Trumbore, 2007; Carbone *et al.*, 2007).

### *Belowground C cycling*

In contrast to most seasonally dry ecosystems, surface litter moisture was enhanced by regular fog drip, condensation of dew, high humidity, and reduced evaporative demand in summer. The pattern of C loss from the soil surface was strongly controlled by the timing of fog drip inputs. More total soil respiration, and a greater contribution from heterotrophic respiration, was observed at Sauces over both summers. This is consistent with the observed lower soil organic C content in the upper soil layers, even though pines were more productive at Sauces. It also supports previous observations that summer fog drip primarily stimulates heterotrophic decomposition of soil organic matter (Carbone *et al.*, 2011) and follows the more generalized pattern of heterotrophic contributions increasing in more mesic ecosystems (Subke *et al.*, 2006). Broadly, these results suggest that with more fog or wetter conditions, litter layer soil microbes increasingly dominate heterotrophic C cycling dynamics. Whereas, with less fog or drier conditions, microbes in the mineral soil, where environmental conditions are less variable and more favorable, increase in importance to overall heterotrophic dynamics even though soil C and N are more limited.

The large increase in heterotrophic respiration with increased fog drip at Sauces in 2009, which was not observed at Upper Embudo, was notable, even though microbial biomass C increased similarly in the litter layer at both sites. This result is consistent with parallel laboratory incubations, in which microbial biomass was strongly correlated with respiration in the Sauces litter layer, whereas no relationship was observed in the Upper Embudo litter layer (Boot *et al.*, 2010). Although these results suggest a smaller (in terms of biomass) but more active microbial community at Sauces, they do not indicate the mechanistic processes controlling soil C cycling at Upper Embudo. For example, although there was more fog drip in 2009, it came in fewer and larger events, and overall the litter layer at Upper Embudo was less often wet (Table 1). Differences in these environmental conditions (e.g., moisture availability and frequency of moisture inputs) may result in functional and/or phylogenetic dissimilarities in microbial communities not observable with our biomass measurements (Fierer *et al.*, 2003; Schimel *et al.*, 2007). For example, the microbial community at Sauces may be better adapted to respond to regular water inputs, whereas the microbes at Upper Embudo may have a higher overall response threshold due to less frequent water inputs (Evans & Wallenstein, 2012). Understanding these mechanisms is integral to predicting C cycling in ecosystems with climate change, as microbial diversity (both functional and phylogenetic) is generally not represented in decomposition and ecosystem C models (Allison *et al.*, 2010).

### *Implications for the future*

The Bishop pine forests on Santa Cruz Island represent an isolated and relict ecosystem from a time when regional climate was likely wetter and less seasonal (Chaney & Mason, 1930, 1933; Raven & Axelrod, 1995). Summer cloud shading and fog drip diminish the seasonality of the present climate on Santa Cruz Island, reducing vulnerability of the forests to summer drought (Fischer *et al.*, 2009). This study provides several lines of insight into how coastal ecosystems may respond to changes in cloud cover and precipitation in a future warming world. First, winter rainfall appears to be an important driver of pine activity, whereas summer fog drip strongly influences microbial activity. To our knowledge, winter rain and summer fog frequency are not physically linked in any dynamic way. For example, foggy summers are not correlated with rainy winters, nor are they correlated with dry winters (Williams, 2009). Therefore, these are distinct and temporally offset moisture controls that could affect plant and microbial metabolism differentially in the future. Second, differences in the moisture regimes between the two sites (total available, seasonality, frequency, and intensity of precipitation inputs) were large enough to result in different microbial functioning in the litter and upper soil layers. This reinforces the need for greater knowledge of microbial community responses to drought and water pulses to understand ecosystem C cycling responses to climate change (Fierer *et al.*, 2003; Schimel *et al.*, 2007; Lawrence *et al.*, 2009) and for specific interactions between plants and microbes that might affect plant responses to stress (Friesen *et al.*, 2011). Third, increased fog and stratus cloud cover resulted in enhanced microbial decomposition and less soil organic matter accumulation, yet we do not know how this in turn affected nutrient availability to the pine trees. Thus, cloud-mediated ecosystem feedbacks between free-living microbes, plant-associated microbes, and plants may be important.

In summary, low stratus clouds are prominent in many coastal climates. This research characterized the influence of these clouds on the functioning of a pine forest ecosystem. To our knowledge, this was the first study to assess how clouds affect microbial dynamics and belowground C cycling. We demonstrated that differences in summer stratus frequencies contributed to large differences in plant and microbial metabolism.

These results expand our basic understanding of coastal ecosystems by integrating information on tree growth, belowground C cycling, and microbial responses, and are directly relevant to predicting how these ecosystems may respond to a changing climate. More broadly, we demonstrated that small changes in a subtle aspect of climate, specifically cloud cover, can lead to large microclimate gradients and functional differences in ecosystem C cycling. These results are important because changes in coastal stratus frequency (or perhaps simple changes in cloud height) would alter drought vulnerability for both plant and microbial populations, and would impact the ecological functioning of these unique ecosystems and other coastal ecosystems.

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